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ZOOGEOGRAPHY AND GEOGRAPHIC VARIATION OF *ATLAPETES RUFINUCHA* (AVES: EMBERIZINAE), INCLUDING A DISTINCTIVE NEW SUBSPECIES, IN SOUTHERN PERU AND BOLIVIA

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Abstract.—A distinctive new subspecies, *Atlapetes rufinucha terborghi* (Emberizinae), is described from the isolated Cordillera Vilcabamba, a spur range of the Andes in Dpto. Cuzco, Peru. This population is isolated from the nearest populations of *A. rufinucha* by more than 200 km, and intervening areas with suitable habitat are inhabited by another species, *A. schistaceus*. The new taxon is greener breasted than any other subspecies of *A. rufinucha*. The four subspecies found in southern Peru and Bolivia represent four discrete phenotypes with respect to plumage. Geographic variation in size in the southern Andes does not support Bergmann's Rule.

The Cordillera Vilcabamba, Dpto. Cuzco, Peru, is a mountain range isolated from the main chain of the Andes by deep river valleys with tropical, non-montane habitats (Terborgh 1971, Haffer 1974). Although specimens of birds collected there in the late 1960's by John Weske and John Terborgh have yet to be analyzed in a systematic manner, some endemic taxa have been or are being described: *Schizoeaca vilcabambae* (Vaurie et al. 1972, Remsen 1981), *Cranioleuca marcapatae weskei* (Remsen 1984), *Ochthoeca fumicolor* subsp. nov. (P. Hosey, in litt.), and *Coeligena violifer* subsp. nov. (J. Weske and J. P. O'Neill, pers. comm.).

While examining specimens of Andean *Atlapetes* for a project on their patterns of distribution (Remsen & W. S. Graves 1994), I found five specimens of *A. rufinucha* collected by Weske and Terborgh in the Vilcabamba that represent an important range extension for this species. Furthermore, these specimens differ distinctly from any other population of *A. rufinucha*, so much so that even with just five specimens, it is clear that they represent a new taxon, which may be known as:

Atlapetes rufinucha terborghi,
new subspecies

Holotype.—American Museum of Natural History (AMNH) #820436; mist-netted by John S. Weske and John W. Terborgh on 22 Jul 1967 in the Cordillera Vilcabamba, 2630 m, Departamento Cuzco, Peru, 12°37'S, 73°33'W. The specimen, prepared by Weske (#1334), is a female in breeding condition (ovary and oviduct much enlarged, largest ovum 8 mm; brood patch present) with a completely pneumatized skull and little fat.

Description.—Capitalized color names are from Ridgway (1912). Crown closest to Hazel, becoming slightly paler (Cinnamon-Rufous) on hind-crown and nape, with some Cinnamon Rufous feathers extending to extreme upper back. Rest of back, upper sides of wings, and tail black, obscurely suffused with olivaceous tones on back and on outer webs of secondaries. Upper tail coverts Olivaceous Black. Lores, broad superciliary, face, and auriculars black, contiguous with black of dorsum at neck, but contrasting with the darker back. Chin and throat Light

Greenish Yellow. Faint, broken malar stripe dark olive. Breast closest to Javel Green. Center of belly like throat, blending to broad, darker, Olive Green flanks and slightly paler undertail coverts. Rather than uniformly colored, the underparts have faint hints of obscure streaks throughout; the breast is not sharply demarcated from the paler throat and belly. Undersides of remiges and rectrices Fuscous. Soft part colors recorded by Weske: iris rich brown; bill black; legs dark brown. Measurements: wing chord 70.2 mm; exposed culmen 18.5 mm; tail 74.2 mm; and tarsus 23.9 mm.

Diagnosis.—*Atlapetes r. terborghi* is greener and darker ventrally over-all than any other subspecies of *A. rufinucha.* It can be distinguished from the nearest population of *A. rufinucha, A. r. melanolaemus* (which *A. r. terborghi* resembles in lacking a loral spot and black feathers on forecrown), by its yellow-green throat and malar area, which is variably clouded with black in *A. r. melanolaemus.* In *A. r. terborghi,* the breast, although greenish and darker than the throat or belly, lacks the variable amount of irregular blackish scalloping that characterizes *melanolaemus.* The nominate subspecies of *A. rufinucha,* from dptos. La Paz and Cochabamba, Bolivia, (which is more similar in plumage to other subspecies of *A. rufinucha* throughout the Andes than either *A. r. terborghi* or *A. r. melanolaemus*) differs from *A. r. terborghi* in the following ways: (1) *A. r. terborghi* lacks the yellowish loral spot of the nominate subspecies; this area is black in *A. r. terborghi*; (2) in *A. r. terborghi,* the chestnut of the crown extends to the bill, whereas in the nominate subspecies the feathers closest to the bill on the forehead are black; (3) the nominate form has a conspicuous black malar stripe, whereas *A. r. terborghi* has only a faint trace of a darker malar stripe; (4) the underparts of the nominate subspecies are a bright yellow, whereas those of *A. r. terborghi* are greener; even in the two most yellow specimens of *A. r. terborghi,* the yellow is paler and more washed out than in the nominate subspecies. The back and uppertail coverts of *A. r. terborghi* are slightly paler than those of *A. r. melanolaemus* or the nominate subspecies; the black of the face of *A. r. terborghi* contrasts with the paler back, whereas there is little or no contrast between the face and back of *A. r. melanolaemus* or the nominate subspecies. In these respects, *A. r. terborghi* resembles distant *A. r. carrikeri* (but *A. r. carrikeri* is much paler-backed, paler-breasted, and smaller in size); such mosaic distribution of characters is a prominent feature of geographic variation in *A. rufinucha* (Paynter 1978).

Distribution.—Cordillera Vilcabamba, Dpto. Cuzco, Peru.

Paratypes.—Four other specimens were also mist-netted in the Cordillera Vilcabamba by Weske and Terborgh and prepared by Weske: (1) AMNH 820438, 2620 m, 12°37′S, 73°33′W, male, 18 Jul 1967; (2) AMNH 820437, 2620 m, 12°37′S, 73°33′W, male, 30 Jul 1967; (3) AMNH 820609, 3300 m, 12°36′S, 73°30′W, female, 17 Jul 1968; and (4) AMNH 820633, 3500 m, 12°36′S, 73°29′W, female, 31 Jul 1968. The two males are darker below than the holotype, with the underparts more heavily suffused with green; the two females are paler than the holotype, with brighter yellow throats and bellies. The holotype, a female, was selected partly because it is intermediate in ventral coloration, although closer to the two males. One female paratype (820609) has a trace of the yellow loral spot and a few black feathers on the forecrown, characters more fully developed in other subspecies. Soft part colors were not recorded on any of the paratypes, but in the dried study skins, the bills, tarsi, and toes appeared identical in color to those of the holotype. Measurements of the paratypes and holotype are in Table 1.

Etymology.—It is a pleasure to name this distinctive taxon endemic to the Cordillera Vilcabamba for the person who engineered

and conducted its ornithological exploration, Dr. John W. Terborgh. The survey of the Vilcabamba by Terborgh and John Weske represents the most rigorous and well-executed inventory of any area of the Andes. The name is particularly appropriate because patterns of distribution of brush-finches in the Andes provide evidence for the influence of interspecific competition on their zoogeography (Remsen & Graves 1994), a major theme of Terborgh's (1971) research in the Vilcabamba.

Natural History

The only information available comes from the specimen labels. Four specimens were mist-netted in humid, montane cloud-forest and elfin forest, from 2620 to 3300 m, and the fifth was mist-netted in "mixture of tall grassland and elfin forest on crest of mountain range" at 3500 m; Weske (1972) gave the elevational limits as 2520 to 3520 m. All five specimens are adults: for four of the five, skull pneumatization was recorded as "complete," and for the one with no skull notation, the testes were highly enlarged (largest 11 mm). Both males had enlarged testes and cloacal protuberances. The holotype female was also in breeding condition, with the largest ovum 8 mm, but for the other two females, gonad information was recorded as "ovary 5 × 4 mm (not enlarged)" and "ovary 6 mm (not enlarged)." Thus, at least some individuals seemed to be breeding in July, which is during the driest part of the year in the southern Andes (Weske 1972, Fjeldså & Krabbe 1990).

If *A. r. terborghi* is like other subspecies of *A. rufinucha,* then it should be a common, conspicuous species that favors forest edge rather than interior; and it should forage actively, often in mixed-species flocks, from near ground to the subcanopy while searching foliage of trees and shrubs, and epiphyte-covered as well as bare branches (Remsen 1985, Fjeldså & Krabbe 1990).

Table 1.—Measurements (in mm) of holotype and paratypes of *Atlapetes rufinucha terborghi.*

Specimen (AMNH #; sex)	Wing chord	Tail length	Tarsus length	Exposed culmen length
820436; ♀ (holotype)	70.2	74.2	23.9	18.5
820609; ♀	71.5	79.1	25.1	17.9
820633; ♀	72.6	74.2	24.7	18.4
820437; ♂	71.6	76.3	25.0	18.6
820438; ♂	75.3	77.7	25.0	19.4

Geographic Variation

Atlapetes r. terborghi is the northernmost of four distinctive subspecies distributed from about 18°S in northern Dpto. Santa Cruz, Bolivia, north to ca. 12°S in Dpto. Cuzco, Peru. Paynter (1978) summarized plumage features of the three previously described subspecies (the nominate subspecies, *A. r. carrikeri,* and *A. r. melanolaemus*), each of which represents a discrete, strongly marked unit (Graves 1985). The only signs of intergradation between any of the subspecies are as follows. A specimen (Louisiana State University Museum of Natural Science, hereafter LSUMZ, 96808) in a series of 55 of the nominate subspecies from Cotapata, Chuspipata, and Sacramento Alto, Dpto. La Paz, has black scalloping on the breast and an enlarged black malar area, thereby approaching *melanolaemus*; whether this represents intergradation or individual variation within the nominate form cannot be determined.

Specimens from the El Choro area, Prov. Ayopaya, northern Dpto. Cochabamba, are anomalous in their variable crown color. Most show the nearly typical cinnamon-rufous crown of the nominate subspecies, but several are paler to varying degrees. For example, some (e.g., LSUMZ 36861) are notably but not greatly paler, some are paler still (e.g., Academy of Natural Sciences, Philadelphia 134927; Field Museum of Natural History 217844), and two (ANSP 134928, FMNH 217837) are very pale, al-

most as pale as *A. r. baroni* of the Río Marañón valley of Peru.

Atlapetes rufinucha is one of many (but not all; see Graves 1991, Kratter 1993) Andean bird species and superspecies that show geographic variation in body size that contradicts Bergmann's "Rule" (Remsen 1984; Remsen et al. 1991; R. Brumfield, pers. comm; D. Wiedenfeld, pers. comm.). Over the limited latitudinal range of the southern populations of *A. rufinucha* a non-Bergmannian pattern is evident. To illustrate geographic variation in size, I used wing length as an index of body size. For 30 male *A. rufinucha* specimens with body mass data from Dpto. Puno, Peru, to Dpto. Santa Cruz, Bolivia, wing length is significantly correlated with cube root of body mass (Kendall's Tau corrected for ties = 0.27, $P = 0.04$), in spite of the large potential measurement error associated with body mass caused by use of different scales by different workers at different localities on birds that had often been in mist nets for varying periods. However, for 24 females from the same area, wing length is not significantly correlated with cube root of body mass (Kendall's Tau corrected for ties = 0.07, $P = 0.66$). For males, wing length decreases significantly with increasing latitude (Kendall's Tau corrected for ties = 0.14; $P = 0.03$; Fig. 1). For females, wing length also decreases with increasing latitude, but the relationship is not statistically significant (Kendall's Tau corrected for ties = 0.14, $P = 0.10$; Fig. 1). For both males and females, the relationship of wing length to latitude may not be linear; only increased sample sizes from southern Peru and northern Bolivia will determine whether the apparent trough at 14–15°S and consequent bimodal distribution is real or an artifact of low sample size. Elevation is not significantly correlated with wing length in either sex (Kendall's Tau corrected for ties = 0.075 for males, 0.14 for females, $P = 0.27$, 0.09, respectively) or with latitude (Kendall's Tau corrected for ties = 0.013 for males, −0.062 for females, $P = 0.84$, 0.46, respectively).

Interpretation of latitudinal gradients in body size is complex when the populations are not in genetic contact (Graves 1991), as is the case in the four taxa of *A. rufinucha*. In two of the four taxa, sample sizes and latitudinal ranges are large enough to analyze trends within a taxon. In *A. r. rufinucha*, both males and females show a "Bergmannian" trend, but the relationship is not statistically significant (Kendall's Tau corrected for ties = −0.115 for males, −0.155 for females, $P = 0.15$, both sexes). In *A. r. melanolaemus*, both males and females show a "non-Bergmannian" trend, but the relationship is statistically significant only for females (Kendall's Tau corrected for ties = 0.085 for males, 0.50 for females, $P = 0.63$, 0.007, respectively).

Zoogeography

Recent fieldwork in Peru by the Field Museum of Natural History has extended the distribution of *A. r. melanolaemus* north in Dpto. Cuzco to 13°13′S, where John W. Fitzpatrick and David Willard collected specimens at Pillahuata, 2510 m, in the Río Cosñipata valley, near the northern limit of the Cordillera de Carabaya. This locality is about 75 km north of the Marcapata region of southeastern Dpto. Cuzco, the previous northern limit for *A. r. melanolaemus*. Other areas of humid montane forest in Dpto. Cuzco between the Cosñipata valley and the Cordillera Vilcabamba are inhabited by a different species, *Atlapetes schistaceus*. Remsen & Graves (1994) found that *A. rufinucha* and *A. schistaceus* replace each other throughout their extensive Andean distributions; they proposed that these two species were either close relatives and competitors or, conversely, that they were yellow and gray representatives of the same lineage. In either case, *A. r. terborghi* and *A. r. melanolaemus* are separated from each

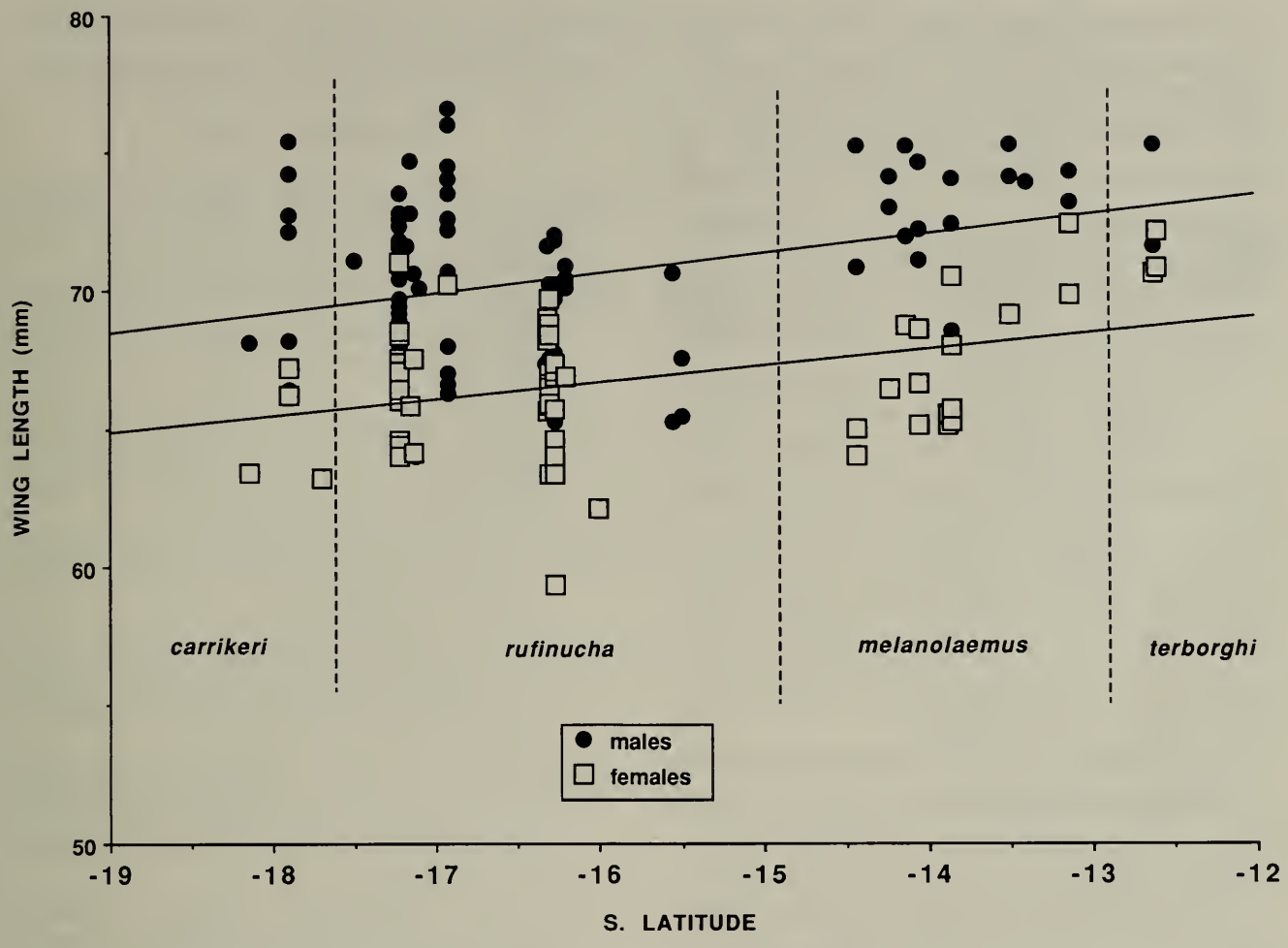

Fig. 1. Relationship of wing length and latitude (degrees S Lat.) for four subspecies of *Atlapetes rufinucha* in southern Peru and northern Bolivia. Latitudes, and elevations for localities not recorded on the specimen labels, were taken from Stephens & Traylor (1983) and Paynter (1992). Vertical dashed lines represent approximate boundaries between four subspecies of region. Diagonal lines represent regression lines of wing length on latitude for males (upper line; $y = 82.1 + 0.72x$, $r^2 = 0.11$) and females (lower line; $y = 76.2 + 0.60x$, $r^2 = 0.13$); lines presented only to illustrate general trends, not formal statistical analyses, because data are largely inappropriate for parametric statistics.

other by more than 200 km, and so *A. r. terborghi* is yet another isolated population of *A. rufinucha* (Paynter 1978). The gap, between the Urubamba-Concebidayoc valley east to at least the Río Vilcanota valley, is inhabited by *A. schistaceus canigenis.* Which taxon of *Atlapetes,* if any, inhabits the region from there east to the Río Yanatili valley and Río Yavero valley, the northwestern limit of *A. r. melanolaemus,* is unknown.

Recent fieldwork in Peru by the Museum of Natural Science, Louisiana State University, has extended the distribution of *A. r. melanolaemus* south to near the Bolivian border, where L. C. Binford and T. S. Schulenberg collected specimens in Dpto. Puno at Valcón, 3000 m, 14°26′S, and Abra de Marucunca, 2000 m, 14°14′S. The southern limit of *A. r. melanolaemus* is unknown but is probably somewhere in northern Dpto. La Paz, possibly the north side of the Río Mapiri canyon, another region virtually unexplored by ornithologists.

Weske (1972) listed one locality record for *Atlapetes tricolor* in the Vilcabamba, at 2100 m, below the lower limit of *A. r. terborghi.* If *A. tricolor* occurs at lower elevations than *A. rufinucha* in the Vilcabamba, then this would represent a similar pattern

in elevational distribution to that in the Western Andes of Colombia and Ecuador, where the two species replace each other at about 2000 m (Remsen & Graves 1994). In central Peru, from central Dpto. Cuzco north to Dpto. Huánuco, *A. tricolor* is replaced at higher elevations by *A. schistaceus.*

Additional recent fieldwork in Peru by the Museum of Natural Science, Louisiana State University, has extended the distribution of *A. r. rufinucha* southeastward from its previous southern limit in Prov. Chapare, Dpto. Cochabamba, Bolivia, into Prov. Carrasco, where C. Gregory Schmitt and Donna C. Schmitt collected a specimen at Quebrada Majón, 6.6 km northwest of Lopez Mendoza, 3150 m (17°32'S, 65°22'W). This specimen is indistinguishable from specimens from Prov. Chapare.

A specimen (LSUMZ 38472) collected by F. Steinbach at San Mateo, extreme eastern Prov. Carrasco, Dpto. Cochabamba, near the Dpto. Santa Cruz border, represents *A. r. carrikeri,* formerly known only from Dpto. Santa Cruz. The specimen matches the type specimen of *A. r. carrikeri* at ANSP (M. B. Robbins, in litt.).

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